

Recurrent Selection for Kernel Weight in Spring Wheat

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ABSTRACT

Increasing kernel weight has been proposed as a method to increase flour extraction in spring wheat (*Triticum aestivum* L.). Recurrent selection was initiated to increase kernel weight while maintaining genetic variation for the unselected traits. Our objectives were to determine (i) genetic gain for kernel weight after eight cycles of selection, (ii) the indirect effects of the selection for kernel weight on other agronomic traits, kernel morphology, milling fractions, and grain protein concentration, and (iii) the level of genetic variability among lines within selection cycles for kernel weight and unselected traits. Ten lines, selected for high kernel weight, were originally intermated to form the base population. About 20 F₂ plants with the highest kernel weight were selected (~2% of the population), and about three of their F₃ progeny were intermated to form the next cycle. This procedure was repeated for eight cycles, with an average of 60 crosses per cycle. Forty random lines from each cycle were used to evaluate agronomic traits in three environments. Kernel weight increased linearly at about 4.5% cycle⁻¹. Cycle means did not differ for plant height and grain yield, but tillers per square meter and kernels per spike decreased 2.4 and 1.6% per cycle, respectively. Spikelets per spike, kernels per spikelet, test weight, and days to heading decreased, whereas spike length increased in response to selection for kernel weight. The proportion of bran and shorts decreased, and flour extraction and grain protein concentration increased 0.58 and 0.16% cycle⁻¹, respectively. No clear trend towards decreased genetic variance for kernel weight was observed since gain was linear over eight cycles. The observed gain from selection and heritability estimates point to kernel weight being controlled by several genes with small effects. Selection for increased kernel size in this population resulted in increased flour yield.

RECURRENT SELECTION is a cyclical breeding strategy designed to accumulate favorable gene combinations while maintaining genetic variability within a population. This procedure is used extensively in allogamous species. Initial studies using this procedure were reported before 1920 and its effectiveness has been documented in the literature (Hallauer, 1985). Recurrent selection has not been as widely used in autogamous species because of the amount of labor required to intermate selected lines and the difficulty associated with producing adequate quantities of seeds for progeny evaluations.

Reported responses in small grains to recurrent selection have been positive (Carver and Bruns, 1993); however, most were short term, usually involving less than five cycles (Goldringer and Brabant, 1993). Parlevliet and van Ommeren (1988) and Marocco et al. (1992)

reported grain yield increased 3.9 and 7.4% cycle⁻¹, respectively, over two cycles of selection in barley (*Hordeum vulgare* L.). Durum wheat (*Triticum durum* L. var. *durum*) grain yield improved 6.3% cycle⁻¹ after two cycles of recurrent selection (Olmedo-Arcega et al., 1995). In spring wheat, Delzer et al. (1995), reported a gain of 2.7% cycle⁻¹ for grain protein after four cycles of selection.

Long-term results from recurrent selection programs involving autogamous crops are limited. A recurrent selection program for grain yield in oat (*Avena sativa* L.) was initiated in 1968 and has completed seven cycles (DeKoeper and Stuthman, 1998). Parents for Cycle 7 produced 21.7% more grain than the parents of Cycle 0, which is nearly a 2.5% yield gain per cycle.

Single trait selection programs often alter other unselected traits, reducing the usefulness of this strategy for cultivar improvement. Recurrent selection for grain yield in oat resulted in increased kernel number and kernel weight, but delayed heading by almost 2 d and increased plant height (Payne et al., 1986). Parlevliet and van Ommeren (1988) reported that although grain yield was increased in spring barley, adverse effects, such as a greater susceptibility to lodging, were also detected. Delzer et al. (1995) reported reduced grain yield, taller plants, and later heading after four cycles of recurrent selection for grain protein content in spring wheat.

Worzella (1942) and Boyce (1948) reported that kernel weight was quantitatively inherited, but postulated major effects by a few genes. Sharma and Knott (1964) reported that kernel weight was moderately to highly heritable (0.37–0.69), depending on the method used to estimate the heritability. Kernel weight was low to moderately and positively correlated with grain yield but negatively correlated with both kernels per spike and number of tillers (Hsu and Walton, 1971; Knott and Talukdar, 1971).

In 1967, a recurrent selection program was initiated to increase kernel weight in spring wheat, leading to a substantial increase in kernel weight after the first four cycles of selection (Busch and Kofoed, 1982). This population has completed its eighth cycle of recurrent selection. Our objectives were to determine (i) genetic gain for kernel weight after eight cycles of selection, (ii) the indirect effects of the selection for kernel weight on other agronomic traits, kernel morphology, milling fractions, and grain protein concentration, and (iii) the level of genetic variability among lines within selection cycles for kernel weight and unselected traits.

MATERIALS AND METHODS

The recurrent selection program was initiated by screening about 100 cultivars and breeding lines for high kernel weight.

Abbreviations: DIA, digital image analysis.

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The 10 selected parents had a mean 1000-kernel weight of 35.9 g and ranged from 35.5 to 37.3 g (Busch and Kofoed, 1982). The parents were intermated in all 45 single cross combinations in 1967 to form the base population. The resulting F_1 progenies were grown in the greenhouse in 1968, and the F_2 populations were space planted with the parents in the field at Fargo, ND, in 1968. About 1000 F_2 plants were harvested, kernel weight was determined on 200 kernels, and 22 F_3 lines with the highest kernel weight were selected as parents to produce the next cycle. Subsequent cycles were generated by intermating selected F_3 lines after growing the F_2 generation in the field. An average selected proportion of about 2.2% provided a minimum of 20 F_3 lines as parents for the next cycle. Baker (1968) showed with Monte Carlo simulations that as few as 20 to 30 pairs of randomly chosen F_2 individuals would approximate true random mating, to the extent that genetic drift would negate the effects of random mating. A minimum of 60 intercrosses was made among the selected F_3 lines with at least three different plants from each F_3 parent. Busch and Kofoed, 1982, give a detailed description of population development.

After the fourth cycle, the program was moved from Fargo, ND, to St. Paul, MN. The original parents and the base population were subsequently lost. From each cycle, 60 F_3 lines were randomly selected and placed in long-term storage. In 1990, these lines were advanced one generation by single-seed-descent and then grown as head rows during a winter increase at Yuma, AZ, in 1990–1991. Ten heads from each F_5 head row were harvested. In the summer of 1991, seed from the bulked heads were grown in two-row plots at St. Paul, MN, to provide adequate seed to conduct replicated field trials.

From each of the eight cycles, 40 F_6 lines were randomly selected. These 320 lines were evenly divided among 10 sets with each set having four lines from each cycle. The hard red spring wheat cultivars Sharp and A99AR were included in each set as checks. Thus, each set contained 34 entries. The 10 sets were grown in 1992 at St. Paul, MN, and Crookston, MN, and in 1993 at Crookston, MN, in a sets-in-blocks design with two replicates in each environment.

In 1992, plots were planted on 5 May at Crookston on a Wheatville loam (coarse-silty over clayey, mixed over smectitic, superactive, frigid Aeric Calciaquol), and on 27 April at St. Paul on a Waukegan silt loam (fine-silty over sandy or sandy-skeletal, mixed, mesic Typic Hapludoll). In 1993, plots at Crookston were planted on 30 April on a Donaldson loam (coarse-loamy over clayey, mixed over smectitic, superactive, frigid Aquic Hapludoll). Plots consisted of two rows, 1.8 m long in 1992 and 2.6 m long in 1993, spaced 0.3 m apart. Broadleaf and grassy weeds were controlled at both locations by recommended applications of herbicides and hand weeding as required. Foliar diseases were controlled with propiconazole (1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]-methyl]-1H-1,2,4-triazole) with one application at Crookston and two applications (one at boot and one at milk stage) at St. Paul. The plots were harvested by combine.

The traits measured on each plot included: grain yield, weight of threshed, cleaned grain; test weight; kernel weight, weight of a 200-kernel sample expressed as weight per 1000 kernels; days to heading, number of days from planting to approximately 50% of the plants with main heads completely emerged from the boot; plant height, average height of two measurements from ground to spike tip, excluding the awns; spike length, average length of five randomly selected heads from the bottom rachis node to the tip of the spike, excluding awns; spikelets per spike, average number of fertile spikelets per spike of five randomly selected heads; kernels per spike, average number of kernels per spike of five randomly selected

heads. Two additional variables were derived from the above traits: kernels per spikelet, determined on the basis of the number of kernels per spike divided by the number of spikelets per spike; and tillers per square meter, computed from grain yield, divided by the number of kernels per spike times kernel weight.

Kernel morphology measurements included kernel area, length, and width of a 200-kernel sample from each plot. Because of labor restrictions only 5 of 10 sets were used, thus sampling 20 of the 40 available lines. Within the three environments, seed from each of the 20 lines from each cycle were bulked across replicates. Digital image analysis (DIA) provided a rapid and accurate characterization of the external morphology of kernels using a method similar to that described by DeKoeper et al. (1993). A Kontron IBAS array processor (Kontron Inc., Echting, Germany) with a 640 by 480 pixel image frame and six image memories was used. Two hundred kernel samples were randomly placed on a light table with substage illumination. The image was captured with a charge-coupled device video camera fitted with a Pentax 55-mm macro lens (Pentax Corporation, Englewood, CO). The camera was properly focused, and both substage and overhead illumination were kept constant during the measurements. The captured image was displayed as a digitized gray level image on a computer monitor. Subsequently, the initial image was subjected to a normalization step that resulted in an image with 256 gray levels. The gray levels were then inverted and segmented into a binary image for measurement. In this segmentation, kernels were automatically discriminated from the background by selecting both high and low gray level thresholds that did not alter the size of the kernels. Area and principle axis length and width of an enclosed rectangle were measured automatically.

Milling fractions were measured at the USDA-ARS Wheat Quality Laboratory at Fargo, ND. The same subset of five sets used for the kernel morphology measurements was used for the milling fractions. Within the three environments, seed from each of the 20 lines from each cycle were bulked across replicates to form a total of 480 samples of 150 g each. The samples were tempered to 155 g kg⁻¹ moisture and milled with a Brabender Quadrumat Senior mill (C.W. Brabender Instruments, South Hackensack, NJ) according to the micromilling method developed by the USDA-ARS Wheat Quality Laboratory (Hareland et al., 2000). Grain protein content was determined by near infrared reflectance spectroscopy following AACC method 39-10 (American Association of Cereal Chemists, 1995).

In the analysis of variance, all sources of variation, except cycles, were considered random. Checks were analyzed across sets to determine whether adjustment of entries within sets was necessary. Assumptions for combining across environments were verified using rankit and residual plots. Levenne's (1960) test was used to test for heterogeneity of error variance across environments. Differences among cycles were tested by an appropriate *F*-test by Satterthwaite's (1946) approximation. Both the linear and quadratic contrasts for cycles were tested against the cycle \times environment interaction mean square. Regression coefficients for regressing the cycle mean on cycle number were derived from appropriate sums of squares. The genetic variance of lines within each cycle was estimated for all traits by estimated components of variance. To allow comparison of genetic variance across traits, broad-sense heritabilities were calculated on an entry-mean basis by variance components (Hallauer and Miranda, 1988). Standard errors of the heritability estimates were calculated as described by Dickerson (1969).

Table 1. Selected mean squares for agronomic traits from the combined analysis of variance † for eight cycles of recurrent selection for kernel weight evaluated in three Minnesota environments.

Source	df	Yield ($\times 10^2$)	Test weight	Kernel weight	Heading	Plant height	Spike length	Spikelets spike ⁻¹	Kernels spike ⁻¹	Tillers m ⁻² ($\times 10^2$)	Kernels spikelet ⁻¹
Cycle	7	16 580	77.6*	208.3**	199.2**	114.6	14.9**	9.4**	206.1**	564.1*	0.45*
Linear	1	26 692	236.9*	14 280.0**	1 272.5**	66.0	84.8**	57.8**	1 206.5**	3 595.0**	1.84**
Quadratic	1	58 234	245.8*	182.5	4.6	105.8	8.2**	0.1	100.5	312.4	1.06*
Cycle \times Environment	14	12 867**	21.4**	37.5**	8.0	143.4**	0.2	0.9*	35.8**	131.9**	0.13**
Cycle \times Set (Environment)	189	3 046	12.7	15.0	3.7	33.5	0.4	0.7	10.3	27.3	0.04
Entry (Set \times Cycle)	240	4 326**	21.4**	25.0**	11.1**	72.9**	0.7**	1.2**	15.4**	29.9**	0.05**
Pooled Error	480	2 686	10.1	10.0	1.3	16.8	0.1	0.3	6.0	20.9	0.02

* Indicates significance at $P \leq 0.05$.** Indicates significance at $P \leq 0.01$.

† Analysis based on entry means from each environment.

RESULTS AND DISCUSSION

On the basis of the analysis of variance of the checks, Sharp and A99AR, no adjustments for sets were needed in the three environments (data not shown). Across sets within environments, no serious outliers, curvature, or nonnormality was detected using residual and rankit plots, respectively (data not shown). Levenne's test indicated heterogeneity of error variance ($P \leq 0.05$) across environments for grain yield, kernel weight, days to heading, and number of kernels per spike. This heterogeneity decreased the power to detect differences among cycles of selection.

The accuracy, reliability, and repeatability of the DIA data were evaluated in several ways. First, one 200-kernel check sample was included at the beginning of each session. The largest standard deviation of the check was observed for kernel area and equaled 1.4% of the overall mean, indicating that no adjustment of the means was warranted. Secondly, the mean for kernel length of 10 samples was compared with the average kernel length as measured by a hand-caliper. The correlation between the two methods was high ($r = 0.98$, $P < 0.01$); however, the caliper-measurement means were consistently 8 to 11% higher. Finally, the effect of orientation of the kernel on the surface of the light table was evaluated. In the method used, the 200-kernel samples were randomly distributed on the surface of the light table without regard to orientation. Samples were measured both in random orientation and with each individual kernel on its crease. With the crease down, the mean kernel length was 8% longer and kernel width was 3% smaller than in the random orientation. Kernel width

was expected to show the most variation due to the random kernel orientation. However, these small differences had little effect on ranking of the entries. DIA was considered a fast and reliable method for determining external kernel morphology, especially since the interest was in the relative change across cycles of recurrent selection.

Selection Responses

Agronomic Traits

Cycle means changed linearly for all traits except grain yield and plant height (Table 1). Kernel weight increased at the rate of 1.7 g cycle⁻¹ or 4.5% cycle⁻¹ (Table 2, Fig. 1), similar to the gain (3% cycle⁻¹) reported for the first four cycles of selection (Busch and Kofoid, 1982). Kernel number decreased at the rate of 0.5 kernels spike⁻¹ per cycle, whereas tiller number decreased 8.4 tillers m⁻² each cycle. Spikelet number decreased linearly at the rate of 0.11 spikelets spike⁻¹ per cycle.

As expected, compensation among yield components occurred because yield did not change across cycles (Table 1). In the developmental sequence, the number of tillers per square meter and spikelets per spike decreased as kernel weight increased, whereas the number of kernels per spikelet decreased slightly in the first few cycles (Table 2, Fig. 1). Since the number of kernels per spikelet did not decrease in later cycles, the reduction in kernel number did not result from increased abortion of developing kernels in later cycles. Thus, fertility did not decrease and competition for resources must have

Table 2. Cycle means of agronomic traits across three Minnesota environments following eight cycles of recurrent selection for kernel weight.

Cycle	Yield	Test weight	Kernel weight	Heading	Plant height	Spike length	Spikelets spike ⁻¹	Kernels spike ⁻¹	Tillers m ⁻²	Kernels spikelet ⁻¹
	kg ha ⁻¹	kg hl ⁻¹	g	days	cm				no.	
1	4065	72.2	37.20	58.1	105.7	7.89	14.3	30.3	347.1	2.12
2	4142	71.6	40.05	58.5	108.3	8.41	14.4	29.6	332.5	2.05
3	3888	70.5	41.20	57.2	107.0	8.44	14.3	28.9	319.1	2.02
4	3845	69.8	42.90	56.2	106.9	8.68	14.0	27.7	309.6	1.98
5	3797	70.4	45.65	56.5	107.5	8.72	14.1	27.2	294.6	1.93
6	3855	70.1	46.85	55.6	105.4	8.89	13.9	26.9	295.3	1.94
7	3920	70.4	47.90	55.4	106.6	8.72	13.7	27.2	290.0	1.99
8	3968	70.4	48.95	54.8	106.1	9.03	13.7	27.1	288.5	1.97
Mean	3935	70.7	43.83	56.5	106.7	8.60	14.0	28.1	308.5	2.00
<i>b</i> (linear)†		-1.16	1.70	-0.50		0.31	-0.11	-0.49	-8.4	-0.09
<i>b</i> (quadratic)†		0.10				-0.02				0.01

† *b* values significant at $P \leq 0.05$ are reported.

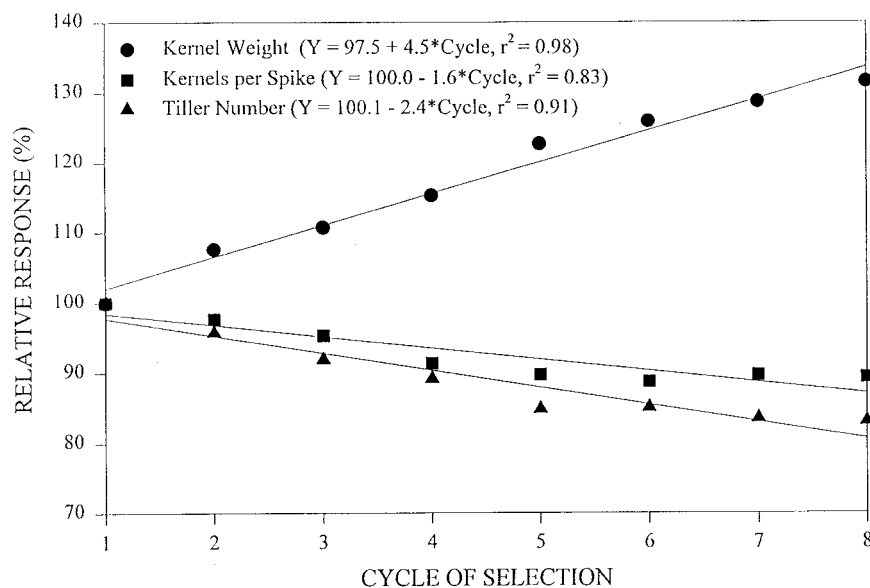


Fig. 1. Response to eight cycles of recurrent selection for kernel weight in spring wheat as a percentage of the Cycle 1 mean for kernel weight, kernels per spike, and tillers per square meter.

occurred prior to grain fill. Since grain yield did not change over cycles, developmental plasticity enabled plants to take alternate pathways and maintain a relatively stable yield level (Adams, 1967).

A quadratic response was detected for test weight, spike length, and number of kernels per spikelet (Tables 1 and 2). Spike length increased from Cycle 1 through Cycle 6, decreased in Cycle 7, but increased to its greatest length in Cycle 8. Number of kernels per spikelet decreased, reaching a minimum in Cycles 5 and 6, but increased in Cycles 7 and 8. As an indirect response to selection, days to heading decreased linearly at the rate of 0.5 day per cycle (Tables 1 and 2). Busch and Kofoed (1982) detected a similar response in this population in the first four cycles of selection. Sofield et al. (1977) reported that the duration of linear growth during grain fill was greatly reduced as temperature increased. Therefore, an indirect response towards earlier heading may be due to the need for a longer effective grain filling period to escape high temperatures later during the growing season. During the winter increase of the lines in Yuma, AZ, under short-day conditions, we observed that the population had shifted from predominantly daylength sensitive in Cycles 1 and 2 to predomi-

nantly daylength insensitive for Cycles 3 through 8. The shift from daylength sensitivity towards daylength insensitivity allows plants to head several days earlier under Minnesota conditions (Busch et al., 1984). This sudden change in daylength response was not associated with a sudden shift to earlier heading in Cycle 3, indicating that other genes also influenced days to heading.

Cycle means did not differ for plant height; however, a cycle \times environment interaction for plant height was detected ($P \leq 0.01$) (Table 1). At Crookston in 1992, with optimum growing conditions, plant height increased slightly as an indirect response to selection (data not shown).

No significant increase in plant height was observed in the other two environments. Busch and Kofoed (1982) reported no change in plant height after four cycles of selection.

Kernel Morphology

Cycle means differed ($P < 0.01$) for kernel area, kernel length, and kernel width, and both the linear and quadratic contrasts were significant for kernel area, length, and width (Table 3, Fig. 2). These indirect re-

Table 3. Selected mean squares for kernel morphology, milling fractions, and grain protein concentration from the combined analysis of variance† following eight cycles of recurrent selection for kernel weight evaluated in three Minnesota environments.

Source	df	Kernel dimension			Milling fraction			Grain protein
		Area ($\times 10^{-2}$)	Length ($\times 10^{-2}$)	Width ($\times 10^{-2}$)	Bran	Shorts	Flour	
Cycle	7	6 227.57**	297.02**	128.19**	117.53**	55.55**	330.00**	10.82**
Linear	1	41 069.45**	1 708.58**	863.11**	416.79*	128.84	1 011.37	66.12**
Quadratic	1	2 508.31**	234.91*	19.75*	36.88	27.32	127.78	0.59
Cycle \times Environment	14	43.11	2.38	0.66	5.06	11.39**	17.36	0.35
Cycle \times Set (Environment)	84	63.99	3.36	0.96	7.70	1.95	13.23	0.28
Entry (Set \times Cycle)	120	86.41**	7.33**	1.73**	12.81**	6.27**	34.59**	0.49**
Pooled Error	240	56.47	1.87	0.85	7.80	2.89	16.83	0.33

* Indicates significance at $P \leq 0.05$.

** Indicates significance at $P \leq 0.01$.

† Analysis based on entry means from each location.

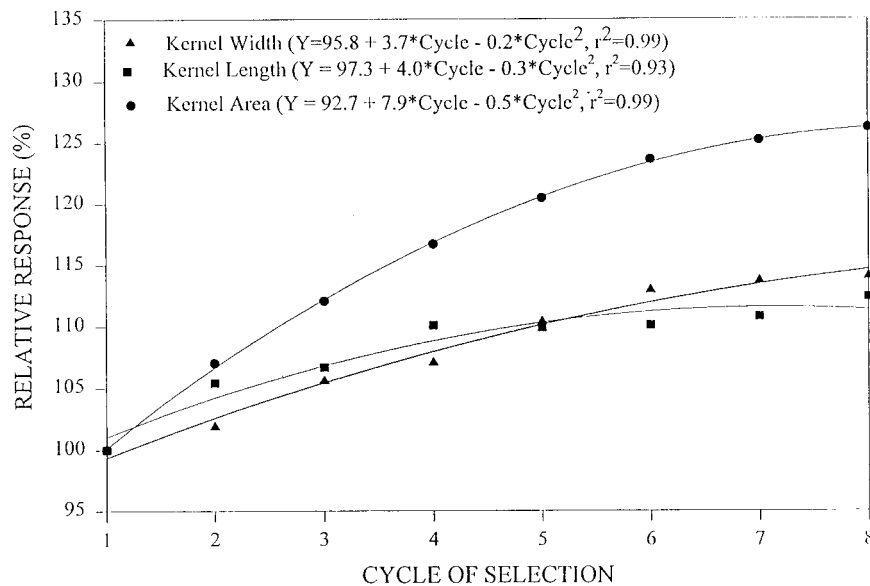


Fig. 2. Response to eight cycles of recurrent selection for kernel weight in spring wheat as a percentage of the Cycle 1 mean for kernel width, kernel length, and kernel area.

sponses decreased slightly over cycles for these three traits. This curvilinear response may indicate that future gain for kernel weight is limited in this population as morphological or physiological limits are being approached (Table 4).

Milling Fractions and Grain Protein Concentration

Cycle means differed ($P < 0.01$) for bran, shorts, and flour content (Table 3). Cycles interacted with environments only for shorts content, but the ranking of cycle means for shorts content at each of the three environments was similar (data not shown). Thus, only the combined analysis and cycle means are presented. The linear contrasts were significant for the three milling fractions bran, shorts, and flour (Table 3). The means of Cycle 2 for bran and flour contents, and to some extent shorts content, deviated from the linear trend (Table 4, Figure 2). Flour extraction in Cycle 2 was equal to the flour extraction in Cycle 8. This deviation was unexpected and no explanation is available. Furthermore, kernels from the later cycles of selection, although larger, physically appeared to have a more wrinkled seed coat than

kernels from early cycles, but this did not appear to affect flour yield adversely.

Both bran and shorts contents decreased while flour extraction increased (Table 4). Eight cycles of recurrent selection for kernel weight has resulted in a population with about 5% higher flour extraction as compared to the first cycle. This increase in flour extraction can be explained as a geometrical function of kernel morphology. Assuming that the outside layers of the kernel that represent the short and bran fraction did not increase in thickness, the volume of the endosperm increased relative to the volume of the outside layers. Thus, with the relative increase in volume of the endosperm, flour extraction increased.

Cycles differed ($P < 0.01$) for grain protein concentration, which increased linearly (Tables 3 and 4). Busch and Kofoed (1982) found that the grain protein concentration increased linearly at the rate of $2.3 \text{ g kg}^{-1} \text{ cycle}^{-1}$ for the first four cycles of recurrent selection. The population continued to increase in grain protein concentration for all cycles of selection. Differences in kernel size and grain protein content relative to position in the spikelets may provide an partial explanation for the

Table 4. Cycle means of kernel morphology traits, milling fractions, and grain protein concentration across three Minnesota environments following eight cycles of recurrent selection for kernel weight.

Cycle	Kernel dimension			Milling fraction			Grain protein
	Area	Length	Width	Bran	Shorts	Flour	
	mm ²	mm		g kg ⁻¹			
1	10.84	5.55	2.70	316	99	585	161
2	11.60	5.85	2.75	276	68	657	163
3	12.15	5.92	2.85	287	81	632	166
4	12.65	6.11	2.89	286	76	638	164
5	13.06	6.10	2.98	284	79	637	170
6	13.40	6.11	3.05	281	75	644	171
7	13.57	6.15	3.07	275	71	654	169
8	13.68	6.24	3.08	271	71	658	173
Mean	12.62	6.00	2.92	285	77	542	167
<i>b</i> (linear) [†]	0.85	0.22	0.10	-4.1	-2.3	6.3	1.6
<i>b</i> (quadratic) [†]	-0.05	-0.02	-0.005				

[†] *b* values significant at $P \leq 0.05$ are presented.

Table 5. Broad-sense heritability estimates and their standard error for agronomic traits evaluated in three Minnesota environments following eight cycles of recurrent selection for kernel weight.

Cycle	Yield ($\times 10^3$)	Test weight	Kernel weight	Heading	Plant height	Spike length	Spikelets spike ⁻¹	Kernels spike ⁻¹
1	0.38 \pm 0.27	0.33 \pm 0.28	0.87 \pm 0.25	0.85 \pm 0.25	0.46 \pm 0.27	0.85 \pm 0.25	0.85 \pm 0.25	0.71 \pm 0.26
2	0.37 \pm 0.28	0.62 \pm 0.26	0.55 \pm 0.26	0.88 \pm 0.25	0.55 \pm 0.26	0.87 \pm 0.25	0.86 \pm 0.25	0.48 \pm 0.27
3	0.30 \pm 0.28	0.19 \pm 0.29	0.73 \pm 0.26	0.90 \pm 0.25	0.85 \pm 0.25	0.84 \pm 0.25	0.82 \pm 0.25	0.55 \pm 0.26
4	0.74 \pm 0.25	0.78 \pm 0.25	0.87 \pm 0.25	0.86 \pm 0.25	0.73 \pm 0.26	0.93 \pm 0.25	0.75 \pm 0.25	0.62 \pm 0.26
5	-0.03 \pm 0.31	0.69 \pm 0.26	0.18 \pm 0.29	0.94 \pm 0.25	0.93 \pm 0.25	0.82 \pm 0.25	0.82 \pm 0.25	0.72 \pm 0.26
6	-0.05 \pm 0.31	0.43 \pm 0.27	0.37 \pm 0.28	0.89 \pm 0.25	0.67 \pm 0.26	0.77 \pm 0.25	0.29 \pm 0.28	0.62 \pm 0.26
7	0.45 \pm 0.27	0.80 \pm 0.25	0.51 \pm 0.27	0.87 \pm 0.25	0.83 \pm 0.25	0.88 \pm 0.25	0.25 \pm 0.28	0.68 \pm 0.26
8	-0.08 \pm 0.32	0.59 \pm 0.26	0.60 \pm 0.26	0.78 \pm 0.25	0.84 \pm 0.25	0.83 \pm 0.25	0.79 \pm 0.25	0.41 \pm 0.27
Mean	0.26	0.55	0.59	0.87	0.73	0.85	0.68	0.60

increase in protein. The proximal kernels within a spikelet are larger and have higher protein percentage when compared to the more distal kernels within the same spikelet (Bremner, 1972; Simmons and Moss, 1978). The number of kernels per spikelet decreased over cycles and was negatively correlated ($r = 0.83$) with grain protein. Thus, a decrease in the average number of kernels per spikelet, resulting in an increasing fraction of proximal kernels, may have resulted in higher grain protein.

Genetic Variance

Heritabilities were highly variable across cycles of selection for kernel weight (Table 5). The heritability of Cycles 5, 6, and 7 did not exceed twice their standard error indicating low, if any, genetic variance since both the error variance and the genotype \times environment interaction effects were relatively constant in each cycle (data not shown). The tendency for genetic variance to decrease in Cycles 5 and 6 was followed by increases in Cycles 7 and 8.

The heritability for kernel weight was 0.44 at St. Paul in 1992, 0.57 at Crookston in 1992, and 0.76 at Crookston in 1993 averaged over cycles. St. Paul was the selection site for the last four cycles of selection, and heritability would be expected to be maximized at that location. However, the heritability estimates of the last four cycles at St. Paul in 1992 were nonsignificant. Genetic variance did not appear to decrease over cycles at St. Paul as heritability estimates were very similar for Cycles 5, 6, and 8 (0.45, 0.48 and 0.49, respectively). No significant genetic variance was detected in Cycle 7 (data not shown).

Kernel length had high heritability estimates, which exceeded twice their standard error for all cycles (Table 6). Heritability estimates for kernel area and width were more variable and often did not exceed twice their stan-

dard error. Heritability estimates for milling fractions and grain protein tended to be lower than those for the kernel morphology traits. There were no well-defined trends across cycles for heritability estimates for any of the kernel morphology traits measured.

Possible causes for the large differences in heritability among cycles for kernel weight and the lack of a consistent trend include (i) genotype \times environment interaction, (ii) sampling error, and (iii) an underestimation of genetic variance due to linkage disequilibrium as a result of the selection intensity. Since the site and year of selection were not the same as the site and year of evaluation, lines within cycles may have responded differentially. Because different environments were encountered when selection was practiced, a biotic or abiotic stress may have resulted in a biased parental selection that increased the genetic variance for kernel weight in the following cycle. The stress may have resulted in selection of lines that were resistant or tolerant to the stress rather than lines with the highest genotypic value for kernel weight, effectively decreasing the selection intensity. Further, the population was moved from Fargo, ND, to St. Paul, MN, after the fourth cycle of selection. This move may have resulted in selection for different genes, and previously selected genes may have responded differently.

The extent to which sampling error may have contributed to the large heritability differences among cycles is not clear. However, 40 randomly chosen lines represented each cycle of selection, which should minimize the likelihood of sampling error. Finally, directional selection may result in an increase in gametic phase or linkage disequilibrium that would reduce the estimable additive genetic variance (Falconer, 1989). This would be balanced by the loss of linkage disequilibrium due to recombination in subsequent generations. Meanwhile,

Table 6. Broad-sense heritability estimates and their standard error on entry mean basis for kernel morphology traits, milling fractions, and grain protein concentration evaluated in three Minnesota environments following eight cycles of recurrent selection for kernel weight.

Cycle	Kernel dimension			Milling fraction			
	Area	Length	Width	Bran	Shorts	Flour	Grain protein
1	0.86 \pm 0.24	0.94 \pm 0.24	0.82 \pm 0.25	0.49 \pm 0.26	0.49 \pm 0.26	0.46 \pm 0.26	0.06 \pm 0.29
2	0.67 \pm 0.25	0.90 \pm 0.24	0.31 \pm 0.27	-0.37 \pm 0.34	-0.59 \pm 0.37	-0.31 \pm 0.34	-0.11 \pm 0.31
3	0.86 \pm 0.24	0.88 \pm 0.24	0.86 \pm 0.24	0.08 \pm 0.29	0.65 \pm 0.25	0.42 \pm 0.26	0.23 \pm 0.28
4	0.63 \pm 0.25	0.85 \pm 0.24	0.60 \pm 0.25	0.77 \pm 0.25	0.70 \pm 0.25	0.73 \pm 0.25	0.53 \pm 0.26
5	0.45 \pm 0.26	0.65 \pm 0.25	0.64 \pm 0.25	0.21 \pm 0.28	0.25 \pm 0.28	0.31 \pm 0.27	0.37 \pm 0.27
6	0.33 \pm 0.27	0.98 \pm 0.24	0.04 \pm 0.30	-0.23 \pm 0.33	0.52 \pm 0.26	0.00 \pm 0.30	0.29 \pm 0.27
7	0.31 \pm 0.27	0.81 \pm 0.25	0.45 \pm 0.26	0.33 \pm 0.27	0.97 \pm 0.24	0.47 \pm 0.26	0.23 \pm 0.28
8	0.56 \pm 0.26	0.88 \pm 0.24	-0.24 \pm 0.33	-0.69 \pm 0.39	0.55 \pm 0.26	-1.28 \pm 0.47	0.53 \pm 0.26
Mean	0.58	0.86	0.44	0.07	0.44	0.42	0.27

response to selection is expected to remain relatively constant until gene-frequency changes increased enough to reduce the response to selection.

The observed gain from selection and heritability estimates point to kernel weight being controlled by several genes with small effects. The effect of individual genes must be relatively similar, since the response to selection was almost constant over cycles even though very little genetic variance appeared to be present in some cycles. However, selection for kernel weight can be described as a function of direct selection for kernel weight and indirect selection against other yield components (Adams, 1967). Thus, even though genetic variance for kernel weight appeared to be exhausted in Cycles 5 and 6, gain could possibly have been maintained because of genetic variance present for the other yield components, whether the relationships among the yield components were physiological or genetic.

The heritability estimates for grain yield did not exceed twice their standard error, except in Cycle 4, indicating that little change in yield would be expected. The heritability of days to heading, spike length, and plant height exceeded twice their standard errors in each cycle indicating that adequate genetic variance was present to allow changes in the cycle means (Table 5). Overall, the heritability estimates indicated that genetic variance appeared to be maintained for most traits except grain yield. However, large differences in heritability were observed from one cycle to the next for both directly and indirectly selected traits while the trait's responses to selection were relatively constant.

Recurrent selection for kernel weight produced linear gain through all eight cycles of selection. Indirect responses to selection have resulted in a Cycle 8 population that is earlier in heading date and has increased spike length and decreased number of tiller per square meter and kernels per spike. Test weight decreased until Cycle 3 but has since changed little while grain yield and plant height were affected little by selection. Grain protein, kernel area, kernel width, and kernel length all increased with selection for kernel weight. Selection for increased kernel size in this population resulted in increased flour yield. The genetic variance, as measured by broad-sense heritabilities, had little predictive value for genetic gains in this population since response to selection was primarily linear while broad-sense heritability fluctuated greatly.

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